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COSMOS CAUDATUS (ASTERACEAE: COREOPSIDEAE) IN MÉXICO: A CYTOTAXONOMIC REAPPRAISAL

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ABSTRACT

Data from cytotaxonomic, comparative flavonoid and greenhouse progeny studies (morphology and reproductive biology) are combined to show that the Mexican populations of the pantropical annual, Cosmos caudatus H.B.K., includes two very distinct species: a relatively small headed, self compatible tetraploid C. caudatus sensu Sherff) which in México frequents the Gulf Coastal Plain from southern Tamaulipas, southward to Chiapas and the Yucatán Peninsula; and a self incompatible diploid, the heretofore undescribed C. pacificus sp. nov., large headed "forms" of which are found along the Pacific slopes of the Transvolcanic Belt in southwestern México State, Michoacán and Jalisco. Additionally, a "small headed" diploid from Chiapas (one known population) that is superficially very similar to nearby C. caudatus populations, is shown to be a geographically isolated member of the C. pacificus complex. The small headed Chiapas diploid is formally described as C. pacificus var. chiapensis var. nov.

KEY WORDS: Asteraceae, Coreopsideae. Cosmos, México.

Cosmos caudatus H.B.K. is by far the most frequently collected and widespread of all Cosmos species. In the western hemisphere, this pantropical annual is especially abundant in Central America and the West Indies, reaching southward to Ecuador, Bolivia, Paraguay, and southernmost Brazil; and northward along the Gulf Costal Plain into southern Tamaulipas, México. Numerous collections are also available from southeast Asia (Philippine Islands, Java, Sumatra, China, India, etc.) where it commonly escapes cultivation.

Throughout its range, *Cosmos caudatus* demonstrates remarkable environmentally induced vegetative plasticity. In lush moist environments it is not uncommon for individual plants to reach 2-3 meters in height and have widely branching, open inflorescences (Figure 1), whereas plants from inhospitable

sites may be accommodated on a single herbarium sheet. Despite such plasticity, *C. caudatus* is rarely misidentified. Its only close relative, the well known, widely cultivated, *C. sulphureus* Cav. (also a pantropical annual weed) has showy heads with distinctive. bright orange ligules, not small heads with short white to pale lavender rays as found in *C. caudatus* (Figures 2A & 3C).

As part of his extensive herbarium studies of the subtribe Coreopsidinae. Sherff (1932, 1955) examined Cosmos caudatus specimens on a worldwide basis. From among this assemblage he recognized not a single intraspecific category. In his very last paper on the Coreopsidinae, however, Sherff (1964) called attention to an annual Cosmos collected near Nuevo Italia, Michoacán, México ($McVaugh \ 18019 \ [MICH]$) that was "very similar to C. caudatus, but conspicuously different as to its achenes, these exaristate even when very young." He noted especially that it was the very first C. caudatus specimen that he had ever observed with awnless achenes. In keeping with his treatments of similar forms in other Cosmos annuals. the McVaugh collection was described as C. caudatus var. exaristatus Sherff. No mention, whatsoever, was made of the floral or vegetative portions of this new variety.

My own field investigations of Mexican Coreopsidinae have revealed numerous Cosmos and Bidens species which include forms with both aristate and exaristate achenes, even within single populations. Indeed, in such populations, it is not uncommon to find awned and awnless achenes within single heads. My initial presumption, therefore, was that C. caudatus var. exaristatus Sherff was just another taxonomically trivial. awnless segregate. Subsequently, however, this view was challenged by the discovery, near the type locality of C. caudatus var. exaristatus, of a remarkable annual Cosmos which combined exceedingly large, showy, lavender raved heads (similar to those of the widely cultivated annual. C. bipinnatus Cav.), with large 2-3 pinnatisect leaves similar to those of C. caudatus and C. sulphureus (i.e., their ultimate segments broadly lanceolate, not linear filiform as in C. bipinnatus). Most interestingly, the chromosome number of this collection (Carman & Gianassi 68-124 (IA) proved to be n=12, not n=24 as was previously reported for C. caudatus (Melchert 1968). A herbarium search stimulated by these observations revealed that morphologically similar plants had been collected previously in México State and Colima, and that the type photograph of var. exaristatus. though not mentioned in Sherff's description, shows the same large raved heads seen on the Carman-Giannasi diploid.

Viewed in totality, these observations suggested that Cosmos caudatus sensu Sherff (1955) might well include two distinct species, a large headed diploid of central México (Sherff's "var." exaristatus) and a small headed tetraploid (the pantropical var. caudatus). To test this hypothesis, populations were sampled across the range of C. caudatus as it occurs in México. At each collection site (Table 1) floral buds were fixed for chromosome studies; bulk floral and vegetative tissues were obtained for comparative flavonoid



Figure 1. Habit of Cosmos caudatus, Gulf Coastal Plain in Veracruz.



Figure 2. Leaf silhouettes and heads of Cosmos caudatus and C. pacificus (photoreduction of field pressed specimens): A = C. pacificus var. pacificus, n=12; B = C. caudatus, n=24. Refer to text for sizes of structures.



Figure 3. Heads of greenhouse progeny of Cosmos caudatus and C. pacificus: A = C. caudatus, n=24; B = C. pacificus var. pacificus, n=12; and C = C. pacificus var. chiapensis, n=12. Refer to text for sizes of structures.

investigations; achenes were collected for establishment of greenhouse populations; and floral heads were preserved (for later measurement) in a premixed solution of ethanol. water and glycerin.

Methods

Chromosome Studies

Freshly collected buds were killed and fixed in modified Carnoy's solution (4 chloroform: 3 absolute ethanol: 1 glacial acetic acid $\lfloor v/v \rfloor$). Young anthers were subsequently removed and squashed in aceto-hematoxylin. Cytoplasmic clearing (and short term preservation) was accomplished by mixing a small drop of Hoyer's mounting medium into the stain before the cover slip was applied. The meiotic chromosome counts obtained and the pairing relationships observed are presented in Table 1 with a list of their voucher specimens (IA). In Table 1, a letter amended to the collection number indicates that the count was made from buds collected from a single individual; counts obtained as populational samples (buds taken from several plants of a single population) are indicated by the collection number only.

Flavonoid Studies

Methanolic extracts were prepared separately for the leaves. rays. and disc floret corollas (including stamens), from individuals of each population listed in Table 1. Using Whatman 3MM chromatographic paper (46 x 57 cm) a two dimensional flavonoid profile of each extract was then developed in TBA (3 tertiary butanol: 1 glacial HOAc: 1 H₂O [v/v]) and 15% HOAc [v/v], long and short runs respectively. All major flavonoids (chalcones, flavones, and flavonols) were isolated from duplicate chromatograms and then characterized via the now standard spectral chemical tests (MeOH, AlCl₃, NaOMe, Ba acetate/borate) described by Mabry, *et al.* (1970). Spectral data available upon request from the author.

Greenhouse Progeny Studies

Greenhouse populations of all *Cosmos caudatus* populations listed in Table 1 were established from seed in the University of Iowa, Botany Department greenhouses and maintained with a vigorous programmed watering schedule on plants of the same age grown under very similar conditions. In addition to allowing direct morphological comparison of living plants, these greenhouse populations were utilized in studies aimed at determining the reproductive

Species	Chrom. no.	Locality		
Cosmos caudatus H.B.K.	n = 24 II	Chiapas: 18 mi E of Cintalapa, route 190, 24 Sep 1966, MSC 6467.		
	n = 24 II	Vera Cruz: 7 mi E of El Mirador, ca 32 mi ne of Coscomatepec, route 125, 15 Oct 71, <i>MBH 71-126</i> .		
	n = 24 II	Vera Cruz: Along local road from Ciudad Catemaco to Lago Catemaco (near Plaze Azul Motel), 16 Oct 1971, MBH 71-132.		
	n = 24 11	Panama: near village of Santa Fe, ca 60 km n of Santiago, 25 Nov. 1979, Roseman <i>538</i> .		
Cosmos pacificus var pacificus Melchert (=C. caudatus var exaristatus Sherff)	n = 12 11	Mexico: 1/2 mi sw of bridge at power plant at Santa Barbara on road from Valle de Bravo, 24 Oct 1971, <i>MBH</i> 71- 236.		
	n = 12 II	Michoacan, ca 28 m s of Uruapan, route 37, 23 Sep 1968, C & G 68-124.		
	n = 12 II	Michoacan: 16.5 mi s of Uruapan, route 37, 25 Oct 1971, <i>MBH 71-248</i> .		
	n = 12 11	Michoacan: 16 mis of Uruapan, route 37, 25 Oct 1971, MBH 71-251a.		
	n = 12 11	Michoacan: 16 mi s of Uruapan, route 37, 25 Oct 1971, MBH 71-251b.		
	n = 12 II	Colima: 11.5 mi w of Jalisco border, route 110, 26 Oct 1971, MBH 71-259.		
Cosmos pacificus var chiapensis Melchert	n = 12 II	Chiapas: 50 mi e of border with Oaxaca, route 190, 17 Oct 1971, <i>MBH</i> 71-161.		

TABLE 1. Meiotic chromosome counts and localities of Cosmos species

MSC = Mclchert, Sorensen and Crawford, 1967 MBH = Melchert, Ballard and Hart, 1971 C & G = Carmen and Gianassi, 1968

Table 1

"strategies" of the plants concerned. Specifically, just prior to anthesis, unopened buds were enclosed in a single layer of cheesecloth. Development (or lack thereof) of achenes in these "bagged heads" was then compared to development of achenes in nonbagged, open pollinated heads. Additionally, individual plants of selected populations were grown in isolated greenhouse compartments. a procedure which precluded cross pollination without having to bag the heads.

Results and Discussion

As shown in Figure 5, the overall ranges of the diploids and tetraploids proved to be quite different. Contrary to our initial expectations, however, the populations sampled in this study fell into three morphological/geographical/ chromosomal subgroupings as follows:

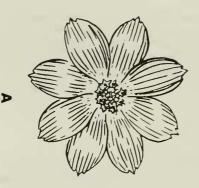
(1) A series of large headed diploids (n=12 II), (Figures 3B & 4A), rays lavender and white respectively) found along the subtropical southern flank of the Transvolcanic Belt from southwestern México State westward into southeastern Jalisco (circles, Figure 5). When fully expanded, the capitula of these diploids are commonly 5-8 cm across the rays, their showy, obovate ligules commonly measuring 20-38 mm long by 11-25 mm wide.

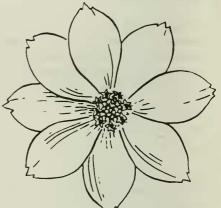
(2) A small headed diploid (n=12 II) Figures 3C & 4B, known from a single collection in Chiapas (Figure 5, note arrow). The heads of these plants (and their greenhouse progeny) were found to be only 2.5-3.8 cm in diameter, i.e., roughly 1/2 the size of the large headed var. *exaristatus*, their narrowly oblanceolate ligules measuring only 11-19 mm long by 7-12 mm wide.

(3) A small headed tetraploid (n=24 II) Figures 3A & 4C, occurring primarily along the Gulf slopes of México from Tamaulipas southward through Veracruz into Chiapas, the Yucatán Peninsula and beyond (Figure 5).

In the field, even before the chromosome numbers of these plants were determined, it was immediately obvious that the plants occurring along the Transvolcanic Belt were part of a totally distinct morphological entity, not just a simple assemblage of exaristate forms. In addition to having some of the showiest heads in *Cosmos*, the ultimate segments of their 2-3 pinnatisect leaves were obviously larger and more confluent than those of *C. caudatus* (or any other *Cosmos* annual [Figure 2A]).

In contrast, the small headed diploid from Chiapas was collected simply as "one additional sample" of *Cosmos caudatus*. i.e., was not recognized as distinct in the field (this erroneous initial identification being influenced, no doubt, by the fact that the plants found at this dry roadside site were rather depauperate and occurred within the general range of *C. caudatus*, only miles from a previously known tetraploid site [Melchert 1968]). However, once attention was focused on this population (because it was unexpectedly diploid) it quickly became evident that its true relationship was clearly with the large







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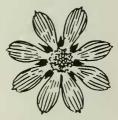


Figure 4. Heads of greenhouse progeny of Cosmos caudatus and C. pacificus drawn to relative scale: A = C. pacificus var. pacificus (white and lavender forms): B = C. pacificus var. chiapensis; and C = C. caudatus. Refer to text for sizes of structures.

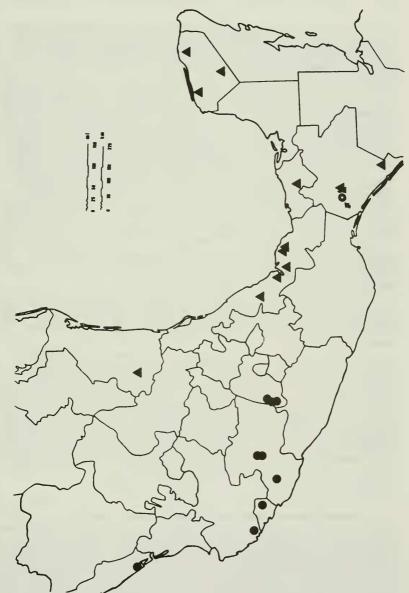


Figure 5. Distribution of Cosmos caudatus (triangles), C. pacificus var. pacificus (circles) and C. pacificus var. chiapensis (starred circle, note arrow).

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headed "var. exaristatus" populations of the Transvolcanic Belt, not with C. caudatus. Features which both demonstrate this alliance and which can be employed as "key" characters to distinguish the diploids (regardless of head size) from the tetraploids follow:

(1) Vestiture - Regardless of head size, the leaves and main stems of the diploids are exceedingly soft velvety to the touch, a somewhat surprising feature since they appear smooth and glabrous to the naked eye. The hairs responsible for this velvety texture, though normally quite dense, are so minute that unless the leaf surface is properly side shadowed, they can be overlooked, even when viewed under a dissecting scope. No other vestiture of this type is known in *Cosmos*. It must be emphasized that this diagnostic vestiture is essentially obliterated by pressing; indeed, it would not have been discovered had it not been for the study of living greenhouse plants. As viewed on herbarium specimens, these tiny hairs appear somewhat appressed and may be shorter than the setae found along the leaf margin. A better (i.e., more easily seen) pubescence feature for identifying herbarium specimens of the diploid is the presence of moderate to dense hairs on both surfaces of the outer phyllaries and the adjacent uppermost portion of the peduncle.

The tetraploids (var. *caudatus*) are essentially glabrous throughout. At most, a very few hairs of moderate length will occasionally be found on the lower leaf surface and/or on the abaxial surface of the outer phyllaries. The leaves of living tetraploids were never found to be soft velvety.

(2) Head configuration - The spatial and relative size relationships between the rays and outer phyllaries, rather than absolute size, are of primary interest here. Regardless of head size, the outer phyllaries of the diploids are much shorter than, and more or less appressed to, the rays which they subtend; the rays themselves widely spreading below, but arching forward above to form a cuplike "corolla" (Figure 4B [Chiapas diploid]). In the tetraploids, the short rays are held in a semi limb/claw arrangement above and apart from the divergent outer phyllaries (Figure 4C [lower]). Because of this arrangement, the outer phyllaries on living heads often equal (or at least appear to equal) the rays, particularly laterally (Figure 4C [upper]).

(3) Reproductive Biology - In the greenhouse, all Cosmos annuals typically produce flowering heads over a period of several months. As the plants age, the heads become progressively smaller, but are otherwise normal. During the fall, when pollinators are still available in our greenhouses, the small headed Chiapas diploids typically set a full head of achenes. When "bagged" with a single layer of cheesecloth, seed set was reduced to a maximum of one or a few achenes per head. In the winter, when pollinators were no longer available, unbagged heads of the same plants never set achenes. The same pattern was noted for all the large raved diploids from south central México.

In sharp contrast, the tetraploids invariably set a full head of achenes, winter as well as summer, bagged or unbagged. In short, the tetraploids are at

least facultatively self fertile, whereas the diploids, like most species of *Cosmos*, (*C. parviflorus* [Jacq.] H.B.K. excepted) are seemingly obligate outcrossers.

(4) Pappus ontogeny - All of the diploid populations were marked by the presence of exaristate achenes. However, contrary to Sherff's description of var. exaristatus as "exaristate from the very first," the disc florets of all diploids studied were typically biaristate at anthesis. During fruit maturation, the awns became thin and variously divergent or reflexed. At this stage they were readily dislodged (some perhaps naturally dehiscent), a developmental phenomenon which results in most mature fruiting capitula typically including a mixture of bi-, mono-, and exaristate achenes. Totally exaristate achenes, although present in certain populations, are the exception.

Ontogenetic awn loss has never been noted among the tetraploids (var. *caudatus*). Indeed, only one of the ca. 500 herbarium collections I have studied was exaristate, this completely so from the very first. Otherwise, the total complement of achenes in each mature fruiting head of var. *caudatus* typically has (1)2-5 stout awns.

(5) Flavonoid Chemistry - Like most other Cosmos species (Melchert, unpublished), the leaves of all diploid populations contained a like complement of 5 or 6 flavonols, all of which proved to be rather ordinary 3-Oglycosides of quercitin and kaemferol. The Mexican tetraploids contained these same flavonols, as their major leaf constituents. However, each added one or more flavone-C-glycosides (vitexin and/or isovitexin) that were not seen in the diploid profiles.

In sharp contrast to the leaves, the rays of both the diploids and tetraploids were dominated, visually by a like set of flavones, 7-O-glycosides of *luteolin* and *apigenin* being the principal components in both. Profiles of all the diploids, however, contained aglycones of these compounds (as minor spots), the tetraploids did not. Additionally, rays of the diploids all contained several *purple* anthocyanins in addition to a set of *pink* anthocyanin spots; the tetraploid profiles showed the same set of pink spots, but lacked the purple ones entirely (none of the anthocyanins was identified spectrally).

Conclusions

When the above data are considered in their totality (Table 2), two conclusions are inescapable. First, the *small headed diploid* population from Chiapas is very clearly part of the *large headed* "exaristatus" assemblage found along the Transvolcanic Belt. Second, the "exaristatus" assemblage is, by reproductive criteria (chromosome number and reproductive biology), as well as phenotypic criteria (morphology and flavonoid chemistry), a distinct species, not just a variety of *Cosmos caudatus*. Accordingly, a complete description of the diploid is rendered here.

TABLE II. Data summary contrasting Cosmos caudatus and C. pacificus.

Data Summary	Cosmos caudatus	Cosmos pacificus	Cosmos pacificus
		var. chiapensis	var. pacificus
Meiotic chromosome complement	<u>n</u> = 24 11	<u>n</u> = 12 II	n = 12 IJ
Reproductive Biology self-compatible	+		
Leaf flavanoids <u>Flavonols</u> Quercitin-3-0-glys Kaemferol-3-0-glycs	+ +	+ +	++
Flavones vitexin and/or isovitexin		+	+
Ligule flavanoids Flavone + Flavonol <u>glvcosides</u>	+	+	+
Flavone + Flavonol aglycones		+	+
Anthocyanins pink spots purple spots	+	:	* *
Pubescence patterns Leaves velvety to touc	h	+	+
Outer involucral bracts pubescent on both surfaces	S	+	+
Head size Diameter across			
expanded ligules	19-27(3.5) cm	(2.5) 3.0-3.8 cm	(4.0) 5-8 cm
ligule length width	9-17 (18) mm 5.0-8.0 (8.5) mm	11-19 mm 7-12 mm	(20-) 25-38 m (9) 11-25 mm

Table 2

Elevation of the varietal name *exaristatus* to specific status, a recommended procedure, is rejected here because the name *exaristatus* is descriptively inaccurate and hence potentially confusing (particularly so because true exaristate forms are found in several related *Cosmos* species).

Cosmos pacificus Melchert, sp. nov. Based on Cosmos caudatus H.B.K. var. exaristatus Sherff, Brittonia 16:66. 1964. TYPE: MÉXICO. Michoacán: Summit of Cañon El Marques, 5 mi n of Nueva Italia; abundant on banks and disturbed ground; ungrazed hillsides in Bouteloua grassland, 450-500 m, 19 Sep 1958, McVaugh 18019 (HOLOTYPE: MICH!; Isotype: F [photograph no. 51415!]).

Tall annuals, single stemmed below, freely branching in the inflorescence, 0.5-2.0 m high; the leaves and stems of living plants with a soft velvety texture. Stems multiridged and multisulcate, moderately or, more often, densely short pubescent, basically terete, but with age (and pressing) becoming somewhat tetragonal, reddish purple anthocyanins may develop along the ridges or throughout. Leaves 2-3(4) pinnate-pinnatisect, long petiolate, broadly triangular, 10-32 cm long (including the 4-12 cm long, pubescent petiole), largest leaves to 20 cm wide; leaf segments broadly lance oblong to ovate oblong, (3)6-10(13) mm wide, 14-18 mm wide when segments confluent, abruptly rounded to sharp, indurated tips, both surfaces with very minute, often somewhat appressed, hairs that are notably shorter than the marginal hairs (though relatively dense these seen only under high magnification); the proximal (i.e., trailing) edge of the lower secondary leaflets or upper primary leaflets frequently, but not necessarily, less dissected than the distal side (this viewed as an entire, winglike margin along the lower side of the secondary or tertiary rachis). Heads radiate, showy, mostly 5.0-8.0 cm across the expanded ligules, aggregated in clusters of 3-6 on elongate naked peduncles, these 6-22 cm long, with scattered multicellular hairs. Ray florets mostly 8, neutral, the ligules white with faint pink anthocyanins along the lower portion of the major veins to very deeply purplish lavender throughout; broadly obovate, 18-38 mm long, 11-25 mm wide, the apex abruptly rounded, usually coarsely tridentate. Involucre dimorphic, the outer bracts green, broadly linear to lance linear, 5-8(10) mm long, 1.5-2.0(2.5) mm wide, 1/2 to 2/3 the length of the inner bracts, much shorter than the rays, short pubescent on both surfaces (the receptacle base and upper portion of the peduncle also pubescent); inner bracts white to yellow, the margins hyaline, reddish anthocyanins may be present at the tip, along the margins, or over the entire surface, (8)10-13 mm long, (2.5)3.0-4.0 mm wide, acute. Disc florets 23-50, the corollas vellow above, whitish below, 4.5-9.5 mm long; filaments of stamens with pilose hairs; anthers (1.8)3.1-5.0 mm long, the terminal appendages (0.6)1.0-1.2 mm long. Pales similar in texture to inner involucre, becoming elongate and narrowed toward center of the

head. Mature fruiting capitula with elongate achene beaks protruding 5-15 mm above the pales; achenes black, (10)13-27 mm long (beaks included), the lower fertile portion fusiform tetragonal, each of the 4 faces with a median longitudinal sulcus (in mature fully expanded achenes, a slender nerve often seen extending the length of this sulcus); the shorter peripheral achenes somewhat incurved, with angled corners, short beaked; beaks antrorsely scabrous, tipped with 1 or 2 divergent to reflexed awns or exaristate (ovaries of disc florets typically biaristate, one or both awns lost during fruit development). Awns thin, easily broken, retrorsely barbed, 2-6 mm long. Chromosome number, n=12 II.

ADDITIONAL SPECIMENS EXAMINED (see also Table 1). MÉXICO. Colima: 8 mi SE of Colima, 450 m, 29 Oct 1962, McVaugh 21979 (MICH, NY). México: Puerto Salitre, District Temescaltepec, 1300 m, 20 Sep 1932, Hinton 1786 (GH, NY); Acatitlán, District Temescaltepec, 12 Oct 1934, Hinton, et al. 6745 (F, GH, US); Sta. Barbara, Sto. Tomás de las Platonos, 1100 m, 11 Oct 1953, Matuda, et al. 30380 (NY, US); Otzoloapan, District Valle de Bravo, 1250 m, 5 Sep 1954. Matuda, et al. 31451 (US); Pungarancho, District Temescaltepec, 22 Sep 1933, G.B. Hinton 4790 (F, GH, MO, NY, US). Michoacán: Aguila, District Coalcomán, 20 m, 21 Nov 1938, Hinton 12632 (GH, NY); 3 km al 5 de Paricuaro, sobre la carretera a Tazantla, 1200 m, 21 Oct 1970, Rzedowski 27983 (IA). Sinaloa: Mazatlán, 1925, J.G. Ortega 5966 (US).

It is important to note that ray color in Cosmos pacificus varies considerably both within and between populations. While the vast majority of plants in the Colima population (71-259) had white or extremely pale pink rays, just the opposite was true in the populations from the state of México (71-236), most individuals of which had deep purple-lavender rays. Flavonoid studies have shown these color differences to be largely superficial. Regardless of color, their 2-10 chromatographic profiles are dominated by identical sets of luteolin and apigenin based glycosides, the overt color differences relating directly to quantitative differences in anthocyanin concentration (Melchert, unpublished).

Cosmos pacificus T. Melchert var. chiapensis T. Melchert. var. nov. TYPE: MEXICO. Chiapas: Route 190, 50 mi E of the border with Oaxaca, "semitropical" vegetation on low mountain slopes, 17 Oct 1971, Melchert, Ballard, Hart 71-161 (HOLOTYPE: TEX!; Isotypes: IA!, MEXU!).

C. pacificus T. Melchert var. pacificus T. Melchert multo similis sed differt capitulis ut maximum dimidio angustioribus (3.0-3.5 mm vs. plerumque 5.0-8.0 mm latis), ligulis (10-)14-21 mm longis, et numero chromosomatibus n=12 II ut var. pacificus (vs. n=24 II ut C. caudatus H.B.K.).

Much resembling var. *pacificus*, but heads at most 1/2 the size of that variety; only 3.0-3.5 cm across (not mostly 5.0-8.0 cm as in var. *pacificus*);

ligules (10)14-21 mm long, 3.0-8.5 mm wide; chromosome number, n=12 II as in var. pacificus, not n=24 II as in C. caudatus.

This small headed phase of Cosmos pacificus occurs some 500 miles to the southeast of the nearest known var. pacificus population, occurring within the "general range" of C. caudatus. Indeed, because of their small heads, herbarium specimens of var. chiapensis look superficially more like C. caudatus than var. pacificus. As noted in the text, however, they are distinguished by the size (Figure 2) and texture of their leaf segments (those of var. chiapensis being soft and velvety to the touch when living, not essentially glabrous) and by the configuration of their heads (cf. Figures 4B & 4C). Given the overall distribution of C. pacificus (Figure 5), additional populations of var. chiapensis might be anticipated in the Sierra Madre del Sur of Oaxaca and Guerrero.

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